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REPRODUCTION IN MARGINAL POPULATIONS OF
THE HISPID COTTON RAT (*SIGMODON HISPIDUS*)
IN NORTHEASTERN KANSAS¹

By

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The northward extension of the range of the hispid cotton rat (*Sigmodon hispidus*) into and across the state of Kansas has been well-documented (Rinker, 1942; Cockrum, 1948; Genoways and Schlitter, 1967). Because this species is subtropical in origin and affinities (Hooper, 1959; Hibbard, 1960), populations along the periphery of the range have had to adapt to increasingly temperate environments as they dispersed northward. These environments are characterized by increased seasonal variability, lower winter temperatures, and protracted periods of intense cold. Extreme cold is known to be stressful to individuals of this species (Dunaway and Kaye, 1961) and is believed to be at least partially responsible for dramatic winter reductions in densities observed in cotton rat populations (Gier, 1967; Hoffmann and Jones, 1970; Fleharty *et al.*, 1972).

Climatic conditions in Lawrence, Kansas, are harsh for a large portion of the year and may be extremely severe for several days at a time. The ecological marginality of this locality for *Sigmodon hispidus* is further suggested by the occurrence of local extinctions of cotton rat populations in the area (Gier, 1967; Fleharty *et al.*, 1972; N.A. Slade, pers. comm.).

¹ This study is part of a dissertation submitted by L.R.M. in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Systematics and Ecology, University of Kansas.

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In marginal environments, a reproductive strategy in *S. hispidus* should be evolved which will maximize reproductive success by counteracting the effects of environmental stress and unpredictability. Randolph *et al.* (1977) have described energy costs of reproduction in *S. hispidus* and have discussed the importance of energy allocation as a component of the reproductive strategy of the species in temperate regions. In this paper, we shall examine other mechanisms by which reproductive success in marginal populations of cotton rats may be enhanced. These mechanisms include: increased litter size, alteration of sex ratio to favor females, and lowering of the age at sexual maturity. We shall then compare reproduction in *S. hispidus* in northeastern Kansas with patterns of reproduction in cotton rat populations from other geographic areas (Haines, 1961; Goertz, 1965a, b).

MATERIALS AND METHODS

Monthly samples of *Sigmodon hispidus* were taken for one year (May 1972 through April 1973) from six sites in Douglas, Jefferson, and Leavenworth Counties in Kansas. These sites are within a 20 mile radius of Lawrence in northeast Kansas. A trapline of between 40 and 100 Sherman live-traps baited with crimped oats was set at each site. Traps were set continuously for three nights and were checked every morning and afternoon, with captured animals being removed as they were encountered. Each area was trapped at three-month intervals to minimize the effect of the removal of animals from the population. Monthly abundance estimates were obtained by calculating the number of individuals captured per 100 trap nights in each monthly sample. A total of 384 cotton rats were captured.

Trapping sites are best described as old-fields of cultivated brome (*Bromus inermis*) in early stages of secondary succession. Other common plant species inhabiting these sites include switch grass (*Panicum virgatum*), golden rods (*Solidago* spp.), cord grass (*Spartina pectinata*), and the common sunflower (*Helianthus annuus*).

Following capture, all animals were brought into the laboratory, where they were euthanized, weighed, measured, and then frozen. At autopsy, the following data were recorded for females: (1) relative size of mammae; (2) condition of the pubic symphysis; (3) condition of the vaginal orifice; (4) number of placental scars; (5) number of embryos; (6) embryo weight and crown-rump length; (7) condition of the uterus; (8) number of corpora lutea; and (9) presence or absence of corpora albicantia. In addition, females were classified as to previous reproductive experience as follows: (1) nulliparous—having no embryos, placental scars, and not lactating; (2) primiparous—having one set of placental scars

and corpora albicantia, or having embryos and corpora lutea but no scars or corpora albicantia; and (3) multiparous—having more than one set of placental scars, or having embryos, corpora albicantia, and/or scars. Males were examined for the following: (1) testes position; (2) testes weight and length; (3) weight and length of the vesicular glands; and (4) the presence or absence of convoluted tubules in the epididymis.

RESULTS

Fluctuations in density.—Because reproductive changes are closely associated with density changes in small mammal populations (Krebs, 1966; Keller and Krebs, 1970; Rose, 1974), we examined changes in abundance of *Sigmodon hispidus* in northeastern Kansas over the course of the study. Monthly estimates of abundance are shown in Fig. 1. Cotton rat abundance fluctuated markedly during the study; peaks in abundance were observed in the spring and fall. There was a slight summer decline in abundance and a very precipitous winter decline. Cotton rats were present in all months of the year, although they were only rarely captured in the late winter months. A similar pattern of density changes has been observed by N. Slade (pers. comm.) during a demographic

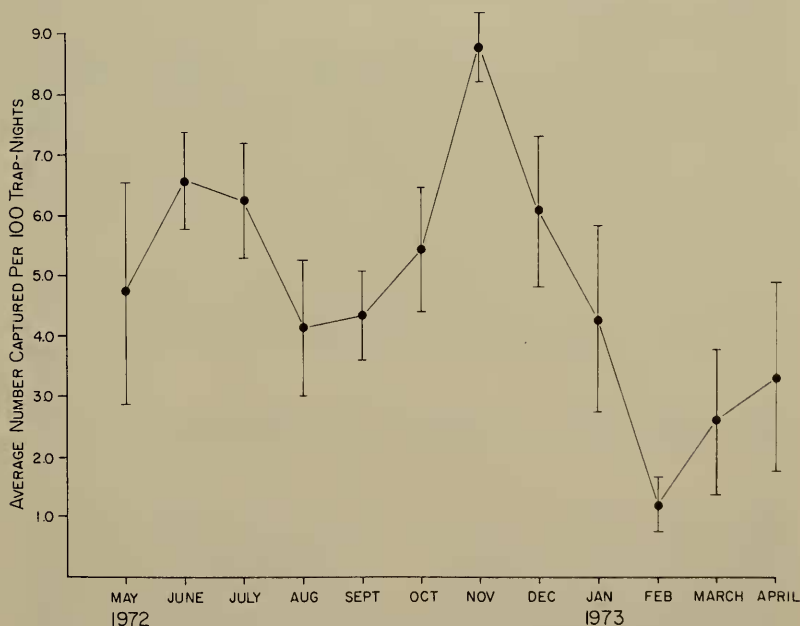


FIG. 1.—Changes in relative abundance of *Sigmodon hispidus* populations estimated by live-trap catches at six areas in Douglas, Jefferson and Leavenworth counties, Kansas.

study of a cotton rat population on the Nelson Environmental Study Area.

Patterns of breeding activity.—The proportions of males and females in breeding condition were calculated for each month to determine temporal changes in population breeding activity. Males were judged to be fertile if the epididymal tubules were convoluted rather than looped (Jameson, 1950). Reproductive activity in females was determined by monthly pregnancy rates based on the proportion of females weighing more than 50 g that were pregnant. One 45g female in the June sample was pregnant, but this would appear to be an exceptional case based on the weights at first reproduction observed in this study and reported by other investigators (Meyer and Meyer, 1944; Odum, 1955; Goertz, 1965a). The percentages of males and females breeding in each month are shown in Fig. 2. The breeding season for *Sigmodon hispidus* is seven months in duration and coincides with the normal frost-free period in northeastern Kansas (April to November). Significant differences in breeding activity between months were observed in males ($\chi^2 = 79.4$; $df = 11$; $P < .005$) and in females ($\chi^2 = 46.8$; $df = 11$; $P < .005$). Temporal changes in breeding activity in males and females appear to be synchronous, although males maintain breeding condition later into the fall and become reproductive earlier in the spring than do females.

Female breeding activity changes closely paralleled changes in density shown in Fig. 1. Peaks in breeding activity in May and September were reflected in the peak densities observed in June-July and November, and the July decline in reproduction occurred just prior to the decline in numbers in August. There was no breeding activity during the winter months, as evidenced by the lack of pregnant or lactating females during this period.

The pattern of breeding activity in males (Fig. 2) is supported by changes observed in average testicular weight. The relative size of the testes was calculated by dividing the testes weight by the body weight. Average testes weights (mg) per 10g of body weight for each monthly sample are presented in Fig. 3. The largest average testicular sizes occurred in June, August, and September. These months were also months of peak reproductive activity as determined by the proportions of fertile males present (see Fig. 2). Testicular regression began in the early fall (October). Smallest testes size was observed in December and the average testes size at that time was only 1/30th the size of testes observed in September. Testes weight increased in the small January and February samples. By April, average testes weight was over 700mg/10g as the breeding season began.

Changes in sex ratio.—One mechanism by which reproductive output can be increased is through the skewing of the sex ratio of

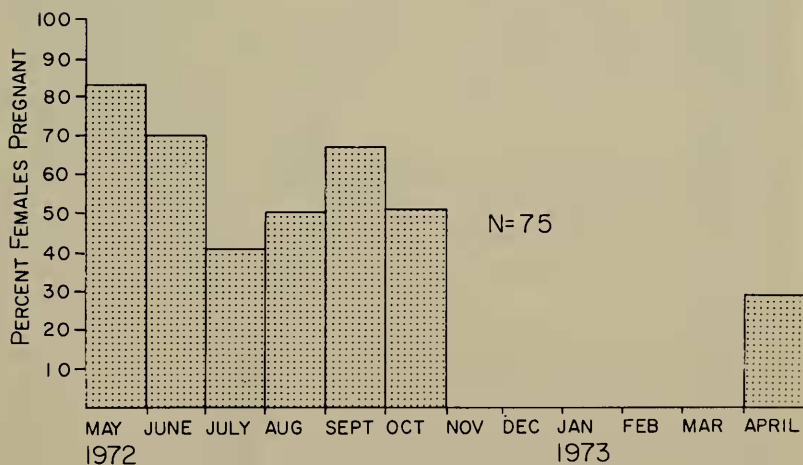
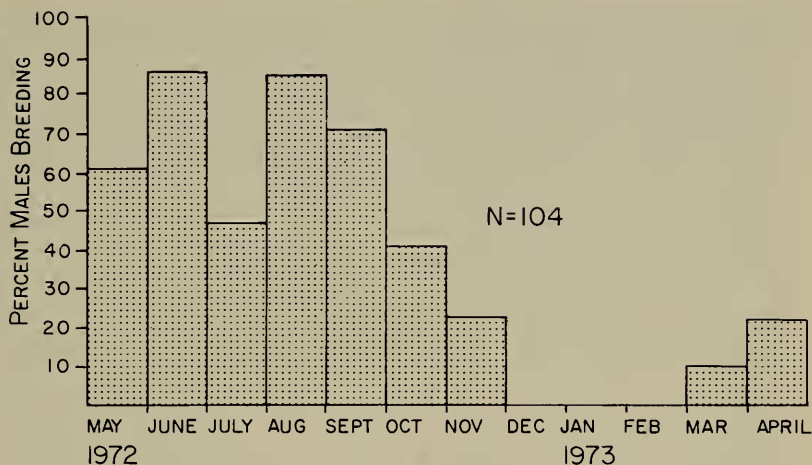


FIG. 2.—Monthly proportions of males and females in breeding condition observed in *Sigmodon hispidus* populations in northeastern Kansas.

a population in favor of females. In this study, males were more abundant than females, with 221 males (57.77%) and 163 females (42.2%) being captured over the 12 month study period. This difference is highly significant ($\chi^2 = 8.76$; $P < .005$). Sex ratio was found to fluctuate from month to month. Ratios favoring males were observed in the winter and fall. Although only one of these ratios was statistically different from 1:1 (June), the trend favoring males in the winter was consistent. However, as the breeding season

progressed, sex ratios became more equitable with equal numbers of males and females being observed.

Changes in uterine litter size.—Pregnant females were separated into primiparous and multiparous groups to analyze changes in uterine litter size. Uterine embryo counts were made for each parity group within each monthly sample containing pregnant females. The mean numbers of embryos for each parity class in each month are given in Table 1. One-way analysis of variance (Sokal and Rohlf, 1969) indicates that the average number of embryos per pregnant female did not vary significantly from month to month for primiparous females ($F_s = 1.49$; $df = 6, 20$; $P < .10$) or for multiparous females ($F_s = 1.41$; $df = 6, 36$; $P < .10$). However,

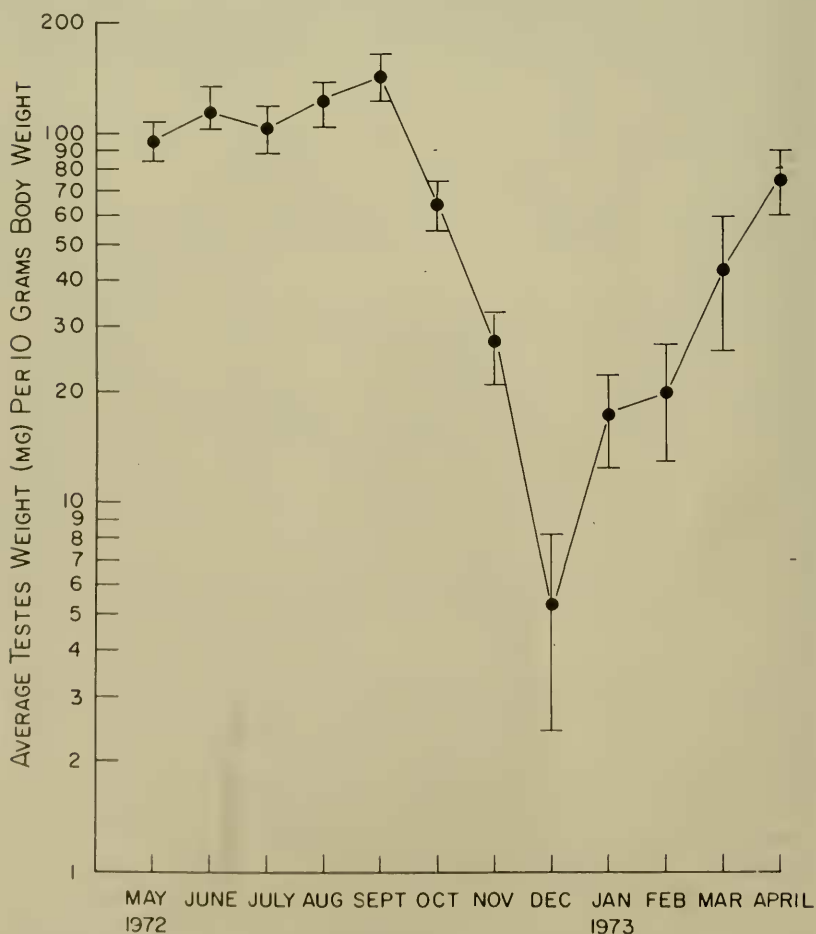


FIG. 3.—Average testicular weights for monthly samples of male *Sigmodon hispidus* from northeastern Kansas.

the average uterine litter size for all multiparous females was significantly larger than that for all primiparous females ($t_s = 3.93$; $df = 68$; $P < .001$). Significant correlations were also observed between litter size and body length ($r = .26$, $df = 68$; $P < .05$) and between litter size and body weight ($r = 0.37$; $df = 68$; $P < .01$). The average uterine litter size for all females was 9.04 ± 0.31 .

Prenatal mortality.—From autopsy of female reproductive tracts, it is possible to quantify prenatal mortality of two types. First, differences in the number of corpora lutea and the number of implantation sites provides a measure of pre-implantation loss. Partial post-implantation mortality (excluding whole-litter loss) can be determined by counting the number of embryos being resorbed. Table 1 provides monthly estimates of the percentage of ova lost via pre-implantation mortality and the percentage of embryos lost through resorption. Low levels of both pre- and post-implantation mortality were observed. Variation between months was non-significant for pre-implantation mortality ($\chi^2 = 2.44$; $df = 6$; $P < .5$) and for post-implantation mortality ($\chi^2 = 5.26$; $df = 6$; $P < .10$). No month showed a loss of ova in excess of 2% and the average loss over all months was 1.21%. An average loss due to resorption of 4.10% was slightly higher than that for pre-implantation mortality but in no month was post-implantation loss greater than 6%. There is no discernible pattern of prenatal mortality with respect to either season or population density.

Median weight at sexual maturity.—Following the method of Leslie *et al.* (1945), a median weight at sexual maturity was calculated. Although some inaccuracy is inherent in using weight as a measure of age in *S. hispidus* (Chipman, 1965), we feel that weight should allow sufficient accuracy to obtain evidence for any seasonal trends in age at sexual maturity.

Animals captured were separated according to sex and then grouped by 20g weight intervals into four-month periods. Female weights were adjusted for all pregnant females by subtracting the weight of the uterus and embryos. The percentage of sexually mature individuals was calculated for each weight class within a time interval. These percentages were then converted to probit values and plotted against the logarithm of average weight of individuals in each weight class. A straight line is fitted and an estimated weight at which 50% of the sample was sexually mature and a standard error of this estimate were calculated. The interval for March 1973 to June 1973 was not included in the analysis because the small sample size of this interval resulted in an indeterminate regression. The median weights at sexual maturity for males and females and their standard errors are given in Fig. 4.

Despite some rather large standard errors resulting from small sample sizes in some intervals, there is a trend towards an increasing

TABLE 1.—Average number of embryos for multiparous and primiparous *Sigmodon* females and estimates of pre- and post-implantation mortality during the breeding season. Sample sizes are in parenthesis.

	May 1972	June 1972	July 1972	Aug 1972	Sept 1972	Oct 1972	April 1973	Total
Mean embryos per multiparous females	8.67 (3)	11.17 (12)	9.14 (7)	8.50 (2)	9.80 (5)	10.17 (12)	7.00 (2)	9.91 (43)
Mean embryos per primiparous females	6.50 (2)	8.29 (7)	7.67 (6)	8.80 (5)	5.00 (1)	7.40 (5)	4.00 (1)	7.67 (27)
% Ova lost	2.43 (41)	1.49 (202)	1.74 (115)	1.61 (62)	0.00 (57)	0.60 (167)	0.00 (18)	1.21 (662)
% Embryos resorbed	2.50 (40)	4.48 (201)	2.65 (113)	0.00 (61)	5.26 (57)	5.92 (169)	5.55 (18)	4.10 (659)

weight at sexual maturity as the breeding season progressed. Throughout the breeding season, both sexes showed this pattern and both males and females became sexually mature at approximately the same weight.

Average body weight.—The reproductive potential of a population is largely a function of the age structure of the population. Since this age structure is rarely, if ever, static, it is necessary to

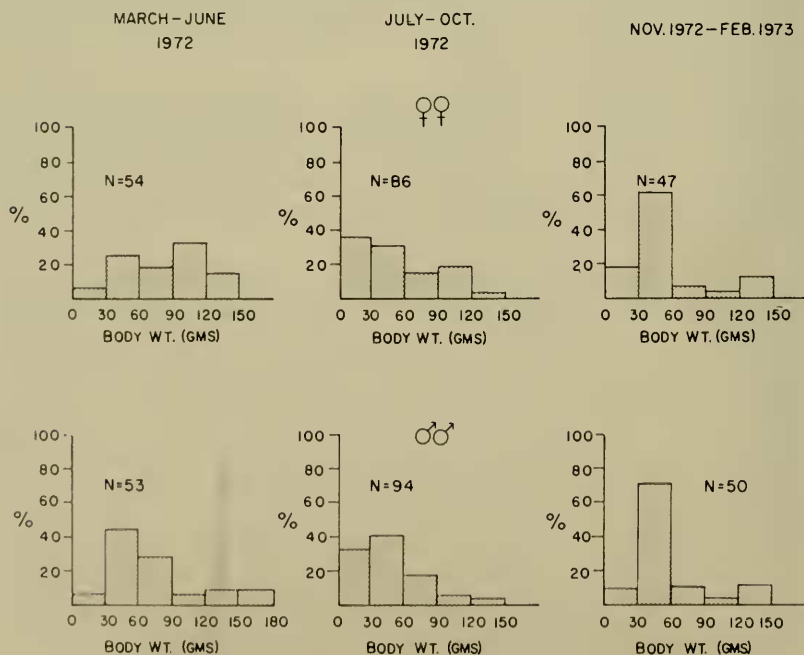


FIG. 4.—Median weights at sexual maturity in males and females in *Sigmodon hispidus*. N is the number in each time interval from which the estimate was obtained.

consider changes in age structure and how these changes might affect reproductive activity. For this study, body weight distributions were determined for each four-month interval, again deleting the March 1973-June 1973 interval because of sample size. Distributions for males and females are given in Fig. 5. In contrast to the pattern exhibited by median weight at sexual maturity, average body weight for both males and females showed a marked decrease as the breeding season progressed. Thus, the age structure of the cotton rat population shifted towards greater proportions of juvenile and sub-adult animals during the breeding season.

DISCUSSION

Cotton rat populations from a number of areas in the United States have been shown to undergo annual cycles in abundance which appear to be associated with local climatic conditions (Odum, 1955; Haines, 1961, 1963, 1971; Goertz, 1964; Fleharty *et al.*, 1972; Joule and Cameron, 1974, 1975) and habitat quality (Goertz, 1964). This annual cycle is characterized by peak densities in the fall, a winter decline, and increasing numbers in the spring and summer. This general pattern was observed in this study for *S. hispidus* in northeastern Kansas. Abundance was lowest in the early spring, and it increased through the summer until peak abundance was reached in the fall. A dramatic reduction in abundance was coincident with the onset of winter and was probably initiated by the cessation of breeding activity. This decline undoubtedly was accelerated by severe winter weather. "Cold weather starvation" (Howard, 1951) may have been a major source of winter mortality since cotton rats are not known to hoard food (Dewsbury, 1970) and extreme cold temperatures restrict foraging activity (Goertz, 1964). Although hard data from this study are lacking, predation may also have contributed significantly to this decline in abundance (Wiegert, 1972).

Reproductive activity was also observed to fluctuate seasonally, with the breeding season restricted to the seven months of the year that are normally frost-free (April to November). Changes in breeding activity were closely associated with abundance changes. Abundance peaks were preceded by periods of intense breeding activity and periods of low breeding activity were followed by reductions in abundance. Changes in breeding activity (Fig. 2) may also be indicative of shifts in population age structure (Fig. 5). For example, the decrease in breeding activity observed in July may reflect the shift from a population composed largely of older, sexually active individuals (spring population) to one in which a large proportion of the individuals in the population are young, sexually immature animals born in the spring and early summer. In contrast, Haines (1961) observed ovulation the year round in

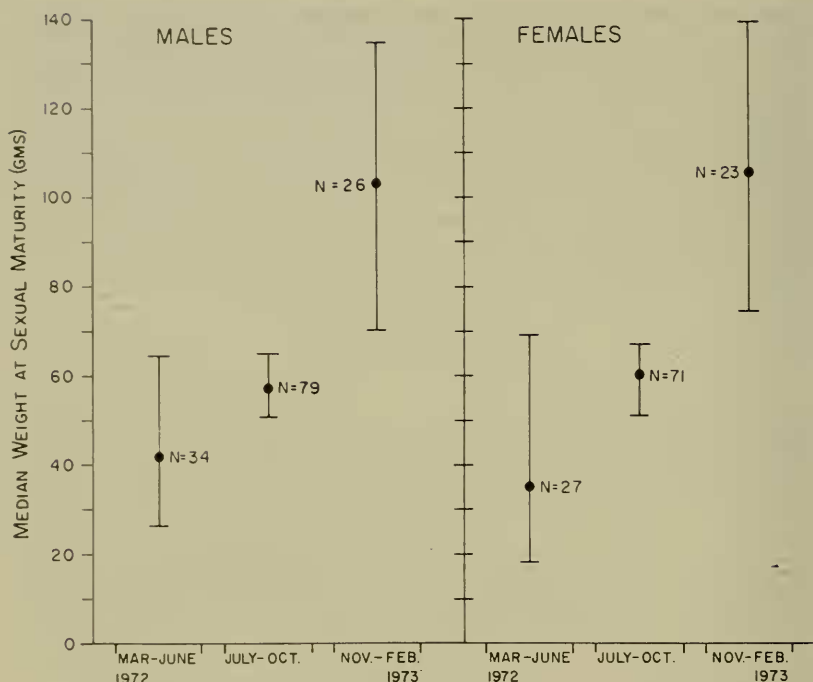


FIG. 5.—Body weight distributions for males and females in a population of *Sigmodon hispidus* from northeastern Kansas.

cotton rat populations near Austin, Texas, and maximum testes size in February. Goertz (1965a) has suggested that, although the incidence of pregnancy and breeding activity declines during the winter, *Sigmodon* populations in Oklahoma are also potentially irruptive throughout the year. Some winter reproduction also takes place in cotton rat populations from Florida (Bigler and Jenkins, 1975) and the Gulf Coast of Texas (G. Cameron, pers. comm.), although the magnitude of breeding activity is reduced. Our data indicate that the cessation of breeding activity in cotton rats in northeast Kansas was complete. Pregnant and lactating females were not present in the population from November 1972 to March 1973. During this time, males showed a pronounced testicular regression and no fertile males were captured from December 1972 to March 1973. It appears that under normal winter conditions, cotton rats in northeast Kansas are not capable of reproduction during the winter. Whether or not reproduction occurs during unseasonably mild winters in Kansas is an open question (Flehart *et al.*, 1972). Having examined temporal changes in abundance and associated changes in breeding activity, we next consider possible

mechanisms by which reproductive output could be increased in these marginal cotton rat populations.

If a species is polygamous, a sex ratio favoring females would increase a population's capacity for growth. However, on a month-to-month basis, only June 1972 showed a sex ratio significantly different from 1:1, and in this month, males were in excess. Biased sex ratio data due to trap type has been reported for several species of small mammals (Keller, 1968; Myers and Krebs, 1972) and *S. hispidus* has shown differential trap response by weight class (Joule and Cameron, 1974). However, we feel that our three-day trapping regime with removal of animals as they were captured provides a reasonably accurate sample of both sexes and weight classes. The excess of males seen in this study is an observation supported by other studies (Goertz, 1965b; Fleharty *et al.*, 1972). One interesting aspect of sex ratio in this study was the statistically nonsignificant but consistent trend towards excess males during the winter and early spring months, ending with the significant difference in June. As the breeding season progressed, sex ratios more closely approximated 1:1. Although accurate survivorship data are not available for our study, the slight excess of males seen through the winter may reflect differential survival with regard to sex. Haines (1972) reported a reduction in longevity for sub-adult females in two separate populations of cotton rats from Texas. However, Goertz (1964) observed no differences in male and female survivorship during a winter in Oklahoma. In any event, equal sex ratios were observed during the major portion of the breeding season and there was no evidence of a shift in sex ratio to favor females and thus increase the population's capacity for growth.

From the uterine litter sizes observed in this study, female cotton rats in northeast Kansas are the most fecund yet reported for the species as a whole (Meyer and Meyer, 1944; Odum, 1955; Haines, 1961; Goertz, 1965a; Bowdre, 1971). Our litter size data support Kilgore's (1970) evidence for latitudinal cline for litter size in *S. hispidus*. Clinal variation in litter size with both latitude and altitude has been reported in a variety of mammalian species (Lord, 1960; Dunmire, 1960; Keith *et al.*, 1966). It would appear that litter sizes in Kansas cotton rats have been increased by natural selection to maximize reproductive success (Spencer and Steinhoff, 1968). However, this conclusion should be qualified since increased reproductive effort *per se* does not necessarily maximize reproductive success or individual fitness. Randolph *et al.* (1977) have reported decreased growth rates in neonatal cotton rats from litters that are larger than average and have pointed out that relative fitness of the young may be subject to maternal energetic constraints during pregnancy and lactation. The extent to which energy allocation to reproduction has been altered to accommodate increased litter sizes

in populations of *S. hispidus* from northeast Kansas is unknown. Some sort of "trade off" between litter size and energy allocation may be important in these populations. As previously suggested (Randolph *et al.*, 1977), insights into the evolution of litter size in cotton rats will come only from comparative studies that include considerations of energetics and the effects of the various biotic and abiotic ecological factors (i.e. spatial and temporal variation in resources, predation, etc.).

Cotton rats from northeastern Kansas displayed a pronounced differential reproductive output based on an individual's parity or previous reproductive experience. Significantly larger litter sizes were observed in multiparous females when compared to primiparous females. Previous studies dealing with cotton rat reproduction (Haines, 1961; Goertz, 1965a) have not considered this relationship and comparative evidence is absent. However, no significant differences in uterine litter size between primiparous and multiparous females were found in 68 pregnant females captured in July 1973 and August 1974 from the states of Veraacruz and Tamaulipas, Mexico, nor was litter size correlated with either body weight or body length (McClenaghan, unpubl.). In temperate latitudes, environmental factors acting as sources of stress may have a more pronounced effect on younger individuals reproducing for the first time and small litter sizes in these individuals may be the result of natural selection operating to enhance the survival of mother and young (Lack, 1954).

Goertz (1965a) and Kilgore (1970) both reported seasonal variability in litter size in cotton rats from Oklahoma and Kansas, respectively. In both these studies smaller litters were produced in the cold weather months and larger litters in warm weather months. Such a pattern was not observed in this study. It is possible that the cotton rat population studied here has become adapted to the environment to the extent that litter size is not affected by climatic conditions. It may also be that the results of Goertz (1965a) and Kilgore (1970) were produced by the parity-dependent reproductive effect described in this paper. Cold weather populations, particularly in late winter and early spring, are likely to be composed largely of primiparous animals born the previous fall, whereas warm weather populations would contain a large proportion of multiparous females. Thus, a cotton rat population's potential for reproductive output would be a function of the age structure of the population and the relative proportions of primiparous and multiparous females.

Prenatal mortality was generally low in the cotton rat populations monitored in this study. Pre-implantation mortality averaged only 1.21% of all ova produced and, of those implanted, an average of 4.10% were resorbed. In comparison, Keller and Krebs (1970)

reported pre- and post-implantation losses in *Microtus pennsylvanicus* from Indiana of 9.0% and 6.4%, respectively. Rose (1974) found these values to be 9.46% and 1.55% in *M. ochrogaster* in northeast Kansas. Kansas cotton rats exhibited no seasonal differences in either pre- or post-implantation loss, suggesting that neither climatic nor density factors play an important role in regulating reproductive output through prenatal mortality.

The average age at sexual maturity has been demonstrated to be one of the most important parameters determining the rate at which a population increases in density (Cole, 1954). Lewontin (1965) has shown theoretically that by reducing the average age at sexual maturity by 10%, a population's potential for increase is enhanced by 100%. Mayr (1963) suggested that there will be selection for an early age at sexual maturity following a rapid decline in numbers in microtine rodent populations or in other species of organisms which are subject to pronounced decreases in density. Cotton rat abundance in northeast Kansas declined rapidly over the winter; after reaching a peak in the fall. Spring cotton rat populations are characterized by low densities following the winter decline and it was at this time that the lowest median weight at sexual maturity was observed. This finding should not be interpreted as selection for an early age at first reproduction in spring cotton rat populations. In fact, these populations are composed entirely of individuals that have survived the winter and are, thus, at least four months old. Rather, this illustrates the fact that cotton rats frequently lose weight during the winter even though they are becoming chronologically older (N.A. Slade, pers. comm.). This observation underscores the need for caution when using weight as a criterion of age in studies of *S. hispidus*. As the breeding season progressed, the median weight at sexual maturity increased while the average population body weight decreased (Figs. 4 and 5). Temporal shifts in body weight distributions like those observed here have been reported for *S. hispidus* in other studies (Fleharty *et al.*, 1972; Joule and Cameron, 1975). Keller and Krebs (1970) have shown that median weights at sexual maturity in populations of *Microtus pennsylvanicus* and *M. ochrogaster* in southern Indiana are lowest following a decline in population density and greatest when the populations are at peak densities. This pattern can be observed in Fig. 4. At least part of the large increase in median weight at sexual maturity seen in the November 1972-February 1973 interval may reflect the decrease in breeding activity in *S. hispidus* associated with the onset of winter. Occurring concomitantly with the cessation of breeding activity in late fall is a noticeable change in the quality of resources utilized by *S. hispidus*. The fall senescence of plant species used as food by cotton rats may act to inhibit reproduction (Negus and Berger, 1977). On the basis of the data

from this study, it is difficult to determine whether the changes in median weight at sexual maturity observed reflected a density-related response or a response to changes in resource quality. It is possible that both these factors are operating in concert on these populations of cotton rats.

In summary, several aspects of reproduction in *Sigmodon hispidus* from northeastern Kansas distinguish these populations from others in different parts of the species distribution. In response to a shortened breeding season and a lack of winter breeding, reproductive output in terms of uterine litter size has been increased to levels not previously reported for the species. In addition, individual reproductive output is dependent to a large extent on previous reproductive experience, with primiparous females having significantly smaller litters than multiparous females. Both these phenomena could be a result of natural selection acting to maximize reproductive success. Reproductive effort has exceeded winter losses on the average, although severe winters probably result in the extinction of some local populations. The end result of these reproductive adjustments is the perpetuation of *Sigmodon hispidus* in temperate regions only recently colonized by the species.

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